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Isolation Mechanisms in Toads of the *Bufo debilis* Group in Arizona and Western Mexico

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More than a century ago Girard (1854) described two small green toads from Mexico. He applied the name *Bufo debilis* to populations "found in the lower part of the Río Bravo (Río Grande del Norte), and in the province of Tamaulipas," and the name *Bufo insidior* to "small specimens, perhaps immature, collected in Chihuahua by Dr. Thos. H. Webb." Boulenger (1882), Cope (1889), and subsequent authors regarded *insidior* as a synonym of *debilis*, until 1938 when Taylor intimated that two species were represented. Taylor ["1936" (1938)] described a third species, *Bufo kelloggi*, based on specimens from Mazatlán and the type from 2 miles east of the city. Boulenger included Sonora in the localities listed for *debilis*, and Cope mentioned a specimen from Mazatlán, Sinaloa, that presumably represents the same population named by Taylor.

Kellogg (1932) listed an individual taken at Mazatlán in 1868, supposedly the same one to which Cope referred 43 years earlier, but Taylor failed to mention the specimen. There are similar inconsistencies in reference to the specimens believed to be the cotypes of *B. debilis* and *B. insidior*. Cope listed two specimens under U.S.N.M. No. 2620 as being taken by Thomas Webb in "Chihuahua, Mexico," whereas Kellogg, who attempted to find out whether the types were extant, stated that U.S.N.M. No. 2620 was collected by Arthur Schott between the Río Salado and

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the town of Camargo in the Mexican state of Tamaulipas. Kellogg could no longer find No. 2620, but under U.S.N.M. No. 2622 he listed two specimens from "Chihuahua: no definite locality," and designated them as the cotypes of Girard's *Bufo insidior*. Cochran (1961) agreed. Kellogg considered eight specimens (designated by Savage, 1954, as "newly metamorphosed") taken by Couch at Matamoros, Tamaulipas, and catalogued as U.S.N.M. No. 2621 to be cotypes of *Bufo debilis*. Cope, however, listed only six specimens under this number, whereas Cochran listed seven. It seems probable that specimens were shifted from one jar to another before tags were attached. In view of the discrepancies in the record, it is questionable whether assumptions concerning the cotypes of *Bufo debilis* and *Bufo insidior* are correct.

It is improbable that the eight newly metamorphosed individuals from Matamoros, which Kellogg regarded as cotypes of *debilis*, provided the basis for Girard's description. From what may be inferred, there is greater likelihood that Girard based his description on adults, possibly including the individual no longer extant that Schott collected between the Río Salado and Camargo in Tamaulipas.

Similarly, there is doubt whether the two cotypes of *insidior* came from the vicinity of the city of Chihuahua, as indicated by Sanders and Smith (1951), though the locality is omitted from their map, or whether the original label merely referred to the state by the same name, as both Kellogg and Savage infer. Nevertheless, *B. debilis insidior* does occur in the immediate vicinity of the city of Chihuahua, and there should be no objection to considering this the type locality. Thomas H. Webb visited the city in 1862 as a member of the United States and Mexican Boundary Commission, and a specimen, A.M.N.H. No. 55274, was taken barely 3 miles north of the city in 1951.

For all practical purposes the precise source of the types is academic. Toads inhabiting humid areas from Tamaulipas northward to southern Kansas differ in some respects from those inhabiting the more arid regions to the west. Though Taylor ["1936" (1938)] resurrected *insidior*, he offered little to substantiate his belief that it represents a distinct species. Bogert and Oliver (1945) suggested that it might prove to be a race of *debilis*, a supposition borne out in subsequent investigations. Sanders and Smith (1951) described an additional race, *retiformis*, and mapped the ranges of the subspecies they recognized, indicating that *insidior* replaced *debilis* not far west of the 100th meridian. Savage mapped the distributions of the two later subspecies and agreed with Sanders and Smith in their assumption that the range of *B. d. retiformis* was contiguous to that of *B. d. insidior* in Arizona and Sonora.

Though Sanders and Smith had but one specimen of *retiformis*, the type, taken 14.4 miles south of Ajo in Pima County, Arizona, they inferred that its range extended southward through Sonora almost to the northern boundary of the state of Sinaloa. In 1951 the nearest record for *Bufo kelloggi* was nearly 700 miles to the southeast in central Sinaloa, but Sanders and Smith offered the conjecture that its range extended to extreme southern Sonora. They indicated that *debilis* was geographically isolated from *kelloggi*, but considered the two most similar in structure. They added that *kelloggi* resembled *retiformis* in pattern, and might "effect a contact," as their map indicated.

Thus, Sanders and Smith regarded *Bufo debilis* as being comprised of four subspecies: *insidior*, *retiformis*, *kelloggi*, and the nominate subspecies. Savage, with 11 additional specimens of *retiformis* obtained in northwestern Sonora, considered *kelloggi* to be more closely related to *insidior*, the range of which was known to extend southward into the state of Durango, approximately 150 miles east of the nearest record for *kelloggi*. Because of "structural differences" between *kelloggi* and *insidior* and the presence of the Sierra Madre Occidental in the area between their respective ranges, Savage inferred that two species were represented. Nevertheless, he suggested that it might be shown that *kelloggi* intergraded with *retiformis* to the north. In view of the lack of material from the intervening area at the time he prepared his manuscript, however, Savage tentatively concluded that *B. kelloggi* and *B. d. retiformis* represented different species. He mapped the distribution of *retiformis*, limiting its range to a small area in northern Sonora, and the adjacent part of Arizona, but suggested that its distribution may extend southeastward along the coastal plain of Sonora, at least to the Río Yaqui.

The year following publication of Savage's views, Riemer (1955) commented on the characters of eight toads taken 11 miles northwest of Vicam in southern Sonora. The locality is roughly midway between the areas known previously to be inhabited by *retiformis* and *kelloggi*. Riemer considered these toads taken near Vicam to be intermediate between *retiformis* and *kelloggi* in several of the characters Savage considered diagnostic. Riemer concluded that the eight toads were best interpreted as intergrades. He rejected Savage's views, therefore, but believed the specimens corroborated the assumption of Sanders and Smith that *kelloggi* was a race of *debilis*.

Meanwhile, however, no specimens of *retiformis* had been reported south of the valley of the Río de la Concepción, more than 200 miles to the northwest. Later Williams and Chrapliwy (1958) reported specimens from four additional localities in Pima County, thus demonstrating a

slight eastward extension of the distribution in Arizona. These authors observed that their specimens appeared to be typical *retiformis* and showed no trend toward *insidior*. Nevertheless they mentioned the supposed intergrades reported by Riemer, and quoted him in support of their belief that *kelloggi* was a subspecies of *Bufo debilis*.

Our knowledge of the distributions of *B. retiformis* and *B. kelloggi* in northwestern Mexico has vastly improved now that paved roads have opened additional areas to exploration during the rainy season. Davis and Dixon (1957) reported *kelloggi* from two localities in Sinaloa and two localities in southern Sonora, and concurred with Sanders and Smith in placing it as a race of *debilis*. Smith and Chrapliwy (1958) reported specimens from northern Sinaloa and southern Sonora. They referred those from Sinaloa to *B. d. kelloggi*, but considered a specimen taken 33 miles south of Navojoa in Sonora to be intermediate between *kelloggi* and *retiformis*. Thus Smith and Chrapliwy offered support for Riemer's interpretation, but suggested that the zone of intergradation is at least 100 miles wide. The nearest published record for *retiformis*, nevertheless, remained more than 200 miles northwest of the area where specimens believed to be intergrades had been taken.

DISPERSALS, DISTRIBUTIONS, HABITS, BEHAVIOR, AND LEVELS OF DIFFERENTIATION

Dispersals and Distributions

As indicated in the preceding review, nearly all students dealing with the two forms, *retiformis* and *kelloggi*, that are restricted to the Pacific drainage regard them as races of *debilis*. Hence they consider *Bufo debilis* a polytypic species comprised of four subspecies.

Within the ranges of the two on the Atlantic drainage, where distributions are mapped in some detail by Sanders and Smith (1951), it is evident that few physiographic or climatic barriers have inhibited their dispersals. The toads appear to be restricted largely to plains, valleys, or the rolling terrain surrounding the higher mountains; they are not encountered on steep slopes or barren rocky terrain. Suitable habitats are usually in areas where shrubs or trees are scattered or absent, usually with grass surrounding the pools used as spawning sites. Though *B. debilis* is absent from such mountain ranges as the Sierra Madre Oriental of northeastern Mexico, it is reasonable to suppose that there are annectant populations between the coastal plain in the Mexican state of Tamaulipas and in the valleys west of the mountains. Genetic continuity between populations in southern Tamaulipas and those inhabiting valleys west of

the Sierra may depend on sporadic expansions of populations along a circuitous lowland route north of the higher mountains, perhaps by way of the Rio Grande Valley. The general north-to-south trend in the mountains and valleys south of the Rio Grande provides a veritable network of lowland habitats suitable for *debilis*.

Though toads of the species can scarcely be expected to occur in all portions of the range, that the distribution of *Bufo debilis* is reasonably continuous may be inferred. The trend toward increasing aridity west of the 100th meridian is paralleled by discernible differences in the pustulation and other external characters of these toads, with sufficient change from one extreme to the other to provide some basis for the recognition of *insidior* as a subspecies of *B. debilis*. The differences observed presumably reflect modifications associated with the adaptations of local populations to either humid or subhumid environments.

The changes in the trend in morphological characters may not be so abrupt, however, as Savage (1954) reported. He noted (p. 100) that "the break between this form [*insidior*] and *debilis* is abrupt in coloration and structure." In a preceding discussion (p. 94) he noted, "the break between the two forms in the United States is abrupt and the area of intergradation appears to be quite narrow," despite having stated in the preceding paragraph (p. 93) that specimens obtained well within the range mapped for *B. d. debilis* possessed "certain characteristics of *insidior*." Populations in the transitional area must, of necessity, be somewhat arbitrarily referred to one subspecies or the other. Aside from minor discrepancies, Savage followed Sanders and Smith in plotting distributions, though trends in the characters subject to variation are not readily indicated by simply mapping distributions.

Sanders and Smith, as well as Savage, mentioned minor differences between local populations, however, and called attention to the increase in the size of *insidior* in examples from the southern extremity of its range. Additional complexities are entailed in recognizing *insidior* as a race of *debilis* if variations within large samples representing local populations are considered. Whether the shift from one character to another is abrupt, or whether the variations encountered are essentially clinal when several characters are considered, there is no reason to doubt (1) that toads in the humid portions of the range (at altitudes below 2500 feet according to Sanders and Smith) tend to differ from those in subhumid regions to the west, and (2) that the distribution of the species is fairly continuous from central Texas westward to southeastern Arizona, and from northwestern Kansas southward to central Zacatecas.

On the Pacific drainage the distributions of toads belonging to the

debilis group are still inadequately known. Nevertheless, specimens obtained by various collectors in Sonora, Sinaloa, and Nayarit since 1955 provide the evidence for significant modifications in the conjectural ranges mapped by Sanders and Smith, and extensions and deletions in the distributions as mapped by Savage. At the western extremity of its range *B. d. insidior* is restricted to valleys, and, though it inhabits areas at elevations above 6000 feet in Mexico, the majority of records from localities on the Pacific drainage in Arizona and New Mexico are little above or below 4000 feet. Stebbins (1951), however, reported a population 16 miles northwest of Pima, at an elevation of approximately 2600 feet in the San Simon Valley, in Graham County, Arizona.

Like toads of the species on the Atlantic drainage, *insidior* avoids V-shaped canyons, but occurs in such places as the upper end of the alluvial fan of Cave Creek, where the stream sporadically flows out of the rugged Chiricahua Mountains at an elevation of 4500 feet, near Portal, Arizona. Toads of the species are not encountered in the canyon above the village, where little open terrain is available. Breeding choruses in the immediate area are restricted chiefly to temporary streams or pools that form during the summer rainy season some 500 feet below Portal on the floor of San Simon Valley.

Thus in southeastern Arizona and the adjacent portion of New Mexico *B. d. insidior* is primarily an inhabitant of subhumid valleys, as it is in Texas and Mexico. It doubtless gained access to the valleys it now occupies largely by following the lowland drainage systems, perhaps occasionally reaching an adjacent drainage by crossing an intervening divide. Lowland habitats suitable for *insidior* are nearly continuous at elevations approximating 4500 feet where the range of this toad extends across the Continental Divide north of the Animas Mountains in southwestern New Mexico. Existing passes in or between the mountains to the west readily account for the penetration of *insidior* into the San Simon, Sulphur Springs, and possibly the San Pedro River valleys of southeastern Arizona.

San Simon Creek and the San Pedro River drain northward into the Gila River, but Sulphur Springs Valley drains into Willcox Dry Lake. Stebbins' (1951) record for *insidior* in the San Simon Valley in Graham County is roughly 100 miles north of the International Boundary, and *insidior* occurs not far south of Willcox Dry Lake in Sulphur Springs Valley. It is improbable, however, that it will be found far north of the boundary in San Pedro Valley, and uncertain that it even reaches this drainage. It remains unreported from such well-known collecting sites in the valley as Fort Huachuca, Fairbank, or Tombstone. (Specimens from Miller Canyon in the Huachuca Mountains to the west of the valley,

reported as "*Bufo debilis*," prove to be juveniles of *Bufo woodhousei*.)

It is questionable whether the two toads Sanders and Smith (1951) reported from "15 miles south of Fort Huachuca" actually came from the San Pedro Valley. If the mileage and the direction are taken literally, the locality falls at the southwestern edge of the Huachuca Mountains, approximately half a mile south of the International Boundary in Mexico. If the collectors recorded the mileage on the road that leads eastward and thence southward from the fort, the toads perhaps came from near Garces on the east side of the Huachucas. Habitats near Garces, however, bear little resemblance to those frequented by *insidior* in the Sulphur Springs and San Simon valleys to the east. If the toads actually came from an area southeast of Fort Huachuca, it is questionable whether it was in the San Pedro Valley.

Whatever environmental changes inhibit the dispersal of *insidior* to the north or to the west, it can scarcely have escaped notice if it occurs along the road traversing the lowlands south of the Rincon Mountains between Benson and Tucson. *Bufo d. insidior* has been taken near Pearce east of the Dragoon Mountains, approximately 80 miles south-southeast of Tucson, but the nearest record for *retiformis* is approximately 100 miles west of the city. There is little if any reason to assume that further collecting will greatly diminish the gap that presently separates the ranges of *retiformis* and *insidior* in the United States.

South of the International Boundary, from Chihuahua and Coahuila southward to Zacatecas (see map, fig. 1), *B. d. insidior* occupies an extensive area on the Atlantic drainage. Records for *insidior* on the Pacific slope are restricted mainly to the Colorado River drainage of southeastern Arizona and the adjacent portion of New Mexico. The only record for Sonora (Savage, 1954), "between Agua Prieta and Fronteras," is not far south of Douglas, Arizona, though it falls on the headwaters of the Río Yaqui, which drains southward into the Gulf of Mexico. The vegetation and drainages in northeastern Sonora, as mapped by Marshall (1957), indicate the probability that *insidior* occupies more extensive areas in northeastern Sonora than our limited knowledge indicates.

Unless *insidior* recently expanded its distribution across the Continental Divide, and more recently from the Colorado River drainage into that of the Río Yaqui, this toad may have penetrated a moderately extensive area west of the Sierra Madre Occidental. As a remote possibility, its range may extend southward through the Río Yaqui Valley to the coastal plain inhabited by *Bufo kelloggi*. Without more detailed knowledge of distributions in northeastern Sonora, it may be unsafe to assume that *insidior* does not intergrade with *kelloggi*. Similarities in their mating calls

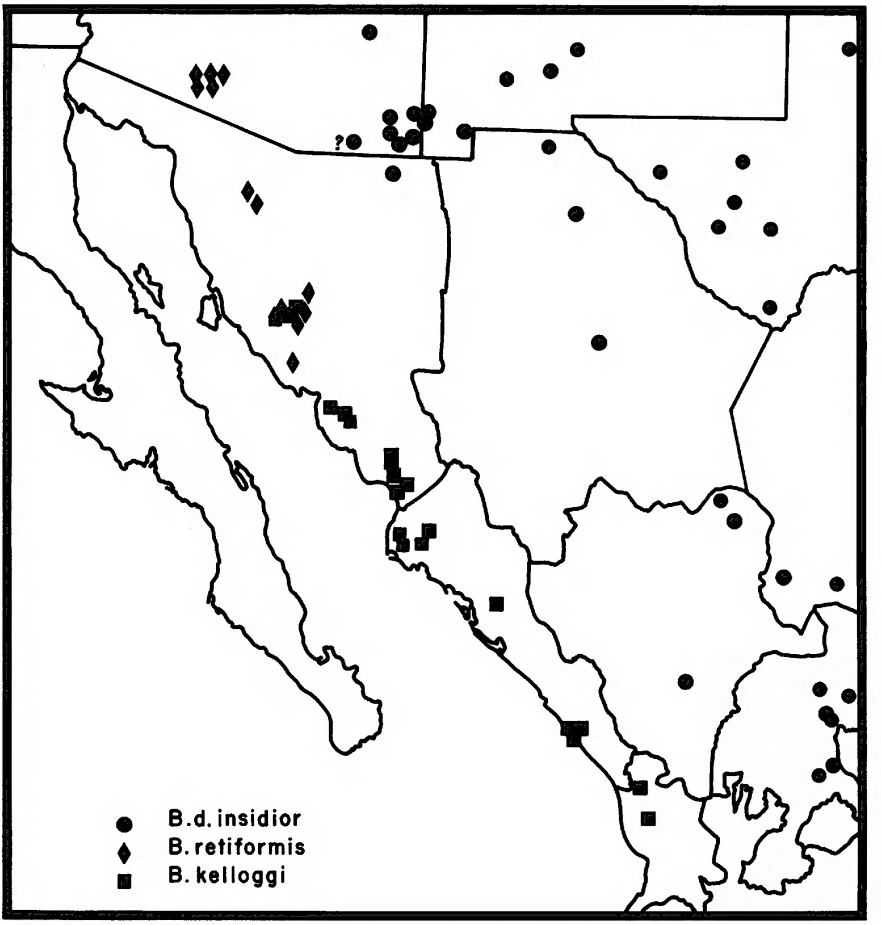

FIG. 1. Map of the regions inhabited by toads related to *Bufo debilis*, including only the western portion of the range of the group, with localities indicating where toads of the three species have been found in the southwestern portion of the United States and contiguous parts of northwestern Mexico.

and behavior suggest that the two might readily interbreed under natural conditions, perhaps more readily than either would interbreed with *retiformis*.

Present records indicate that *Bufo kelloggi* is restricted almost wholly to the relatively narrow Pacific coastal plain of Mexico, between the latitudes of 22° and 29° N., from Rosamorada in Nayarit northwestward through Sinaloa and into Sonora at least as far as Hermosillo. Data indicating that one specimen was taken well inland, "15.2 mi. w. of Ixtlan

del Río" in Nayarit, can almost certainly be attributed to an error in documentation. Accordingly the locality is omitted from the map (fig. 1). In Sinaloa and Nayarit the foothills of the Sierra Madre Occidental rise rather abruptly from the flat, gently sloping, coastal plain. Near the northern extremity of the range of *kelloggi* in Sonora the relatively flat terrain extending inland from the coast is bordered either by steep-sided foothills or by rolling terrain. *Bufo kelloggi* inhabits open, relatively flat areas, in thorn-forest or tropical deciduous forest, seldom if ever above the elevation of 700 feet.

In contrast, *retiformis* is restricted chiefly to rolling terrain, particularly open areas in mesquite-grassland between the elevations of 500 and 1500 feet. Though *B. kelloggi* occurs both to the north and to the south, it has not been taken in the immediate vicinity of Guaymas. There is almost certainly a hiatus in its distribution not far to the north where the coastal plain is interrupted by an irregular ridge surmounted by hills that extends to the coast (see map 1 in Bogert and Oliver, 1945). The population of *B. kelloggi* in the Río de Sonora drainage farther north is presumably isolated from populations inhabiting the flood plains of the Río Matupe, and the Río Yaqui in southern Sonora, with a relatively continuous distribution southeastward along the coast through Sinaloa and well into Nayarit.

The narrow strip of land between the disjunct populations of *kelloggi* in Sonora is inhabited by *B. retiformis*, the distribution of which may follow the mesquite-grassland that covers much of the elevated area extending to the coast. *Bufo retiformis* has been obtained at three localities south of Hermosillo, and a single specimen taken near Rancho Noche Buena, at an elevation of approximately 1500 feet, extends its known distribution to within 20 miles of Guaymas. Northwest of Hermosillo the species has been encountered more often at moderate elevations not far inland from the periphery of the coastal plain. Near the International Boundary in Arizona, *retiformis* occurs at somewhat higher elevations, but not greatly exceeding 1500 feet.

Insofar as records indicate at the present time, *B. retiformis* enters the coastal plain only to the west of Hermosillo. Wells drilled in this area within recent years provide water for irrigation where land is under cultivation. Vast acreages that once supported few Anura may now afford suitable habitats for additional species. Equally important, perhaps, water regularly pumped to the surface during the growing season provides spawning sites where amphibian breeding activities previously were limited by the sporadic and uncertain rainfall characteristic of the region.

Bufo retiformis is ill adapted, or not so well adapted as *B. kelloggi*, to

coastal plain environments, if inferences drawn from distributions provide a reliable index. It is conceivable, therefore, that environmental modifications attributable to irrigation have permitted *retiformis* to invade margins of the coastal plain only within recent years. Our meager knowledge of the situation points to the possibility that the normal habitat of *kelloggi* at the northern periphery of its range is being transformed into one that more closely conforms to the ecological requirements of *retiformis*. It is perhaps significant that the two species are known to occur sympatrically only in the vicinity of Hermosillo, where *B. retiformis* may be replacing *kelloggi* on the coastal plain. Without additional evidence, however, this conclusion must be considered tentative.

Habitats and Behavior

This study was initiated during the summer of 1955, when southern Arizona and the adjacent regions enjoyed unusually heavy rains. Rainfall was heaviest during the latter part of July, with somewhat less precipitation during the early part of August. The breeding activities of *B. d. insidior*, *B. retiformis*, and *B. kelloggi* were observed within a four-day period during the latter part of August. Shortly after the first heavy rains, *insidior* was abundant and calling from numerous spawning sites in the San Simon Valley of New Mexico during the first week of July, and toads of the species continued to call during the first two weeks in August. The other two species, *B. kelloggi* and *B. retiformis*, were observed and collected in the vicinity of Hermosillo, Sonora, during the latter part of July.

Extraordinarily heavy showers on the afternoon of July 27 filled the shallow washes and formed numerous pools in the flat terrain west of Hermosillo. Between 8.00 P.M. and 10.30 P.M., *Bufo kelloggi*, *Pternohyla fodiens*, and *Gastrophryne olivacea mazatlanensis* called from larger pools 17 miles west of the city, where a wash draining from the north crosses the road to Puerto Kino and flows southward into the shallow bed of the Río de Sonora. Other toads, *Bufo cognatus* and *Bufo mazatlanensis*, though encountered on the highway, were not breeding in the area at the time. The immediate region of the spawning site is sparsely covered with vegetation, with creosote bush, desert ironwood, mesquite, and palo verde among the more conspicuous plants. The land near the wash remained unirrigated in 1955, though two *ranchos*, San Carlos and San Antonio, are in the immediate vicinity. Vegetation was somewhat more dense where pools had formed along the wash. Shrubs, along with the debris flooding waters carried into the pools and remnants of grass from the previous year, made it difficult to locate the sources of calls.

Fewer than a dozen male *Bufo kelloggi* were discovered. All of them called from sites at the very edge of the pools, sometimes a few inches above the surface of the water, which they ordinarily faced. Whereas the *Gastrophryne* called from sites hidden in the grass or debris, the toads were all located on muddy banks, in much the sort of situation that *B. d. insidior* frequents in Arizona and New Mexico when issuing its mating call. Mating calls of *B. kelloggi* seem indistinguishable from those of *insidior* when heard in the field, with the observer depending on his recollection of the qualities of the voice of one species. There was no difficulty in distinguishing the call of *kelloggi* from that of *Gastrophryne*, however, though some authors refer to the supposed resemblance. A larger chorus of *Bufo kelloggi*, in which no other species participated, was encountered near midnight on the outskirts of Hermosillo. *Bufo retiformis* was not encountered on the highway, however, and west of the city no choruses of the species were detected in 1955.

On the evening following the discovery of *B. kelloggi* west of Hermosillo, a totally different situation was encountered to the south. The highway leading to Guaymas at first follows a southerly course, winding through low hills between elevations of 900 and 1500 feet. *Bufo retiformis* was first encountered near roadside pools 5 miles south of Hermosillo, where there were loud choruses of *Scaphiopus couchi*. Both species also called 7 miles south of the city, where the mating call of *retiformis* was recorded. The toad was encountered again 11.5 miles south of Hermosillo, in a mixed chorus with *S. couchi*. *Bufo punctatus* called from a ditch that flowed into the pools. Farther south, the road traverses rolling terrain, but no additional choruses were discovered along the road 10 miles farther southward at somewhat lower elevations.

More often *Bufo retiformis* was observed in the immediate vicinity of rain-water sumps, bordered by fresh grass and a few shrubs. Seven miles south of Hermosillo, however, *retiformis* called from both sides of the road, from grass-covered terrain bordering pools to the east, but from the bare, sandy banks of the pools west of the road. In all instances the calling sites were a yard or more from the edge of the nearest pool. The choruses were not large, though only seven males and one female obtained during the evening perhaps represent little more than half of the individuals engaged in breeding activities at the three localities visited. One male left the calling site where it was being recorded and afterward could not be located. Unlike its smaller congener, *B. retiformis* is more inclined to cease calling when approached under the conditions prevailing in small choruses. It is also more difficult to find because it issues its calls at sites distant from the water's edge, usually in grass-covered soil.

None was calling, however, from sites sheltered by shrubs or smaller plants.

The differences in the calling behavior of *retiformis* and that of *kelloggi*, and the apparent restriction of each to separate habitats, as observed in the vicinity of Hermosillo in 1955, provided little support for Riemer's (1955) belief that populations farther south in Sonora could be interpreted as intergrades. On the contrary, the situation suggested that the populations observed in contiguous habitats represented distinct species, readily distinguished by their coloration, pustulation, and mean adult sizes, in addition to the structure of the mating calls and differences in their calling habits. Richard G. Zweifel obtained additional information confirming this interpretation in 1958, though he discovered that the distributions of the two species were not mutually exclusive as the data obtained in 1955 had suggested.

When Zweifel visited the region west of Hermosillo on July 30, 1958, he found the larger toad, *retiformis*, greatly outnumbering *kelloggi*. Near a roadside pond 22.5 miles west of Hermosillo, he first found two females of *retiformis* at 10.30 P.M. A chorus audible in the distance proved to be a quarter of a mile away and centered around a pond estimated to be 200 feet long and 15 feet wide. The chorus was comprised almost wholly of *retiformis*, calling from sites that ranged from a few inches to 30 or 40 feet from the pond. The majority of the males were within a foot or so of the water, however, somewhat closer than those observed in 1955. Several were in amplexus on land, in one instance at least 15 feet from the nearest pool. Zweifel estimates that between 100 and 150 toads participated in breeding activities at this site. He collected 45 males and 25 females, but found only one *B. kelloggi*, a female.

In a somewhat smaller pool nearby, Zweifel counted 37 *retiformis*, and estimated that perhaps twice as many individuals were present. He observed only five male *kelloggi*, all calling from the edge of the pool. Some not calling may have been overlooked. The calls of *kelloggi* and *retiformis* are similar, but when Zweifel heard both species uttering their mating calls simultaneously, he could distinguish the call of one from that of the other. The calls differ sufficiently in pitch for any experienced collector to be able to note differences in the calls under favorable conditions. In the din created by a chorus, however, it might be difficult for some human beings to distinguish one call from the other, despite the magnitude of differences in their emphasized frequencies. Other differences in the call structure are discussed below.

It is pertinent to note that no males of one species were seen clasping females of the other, even when both were present. Thus far no one has

devised experiments suitable to evaluate the importance of differences in calling sites. Though it is questionable whether such behavioral differences are wholly effective in discouraging mismatings, it is probable that they augment the effectiveness of other mechanisms.

The preponderance of *retiformis* in the chorus Zweifel observed might easily have permitted the males of this species to intercept females of the smaller species en route to the pool, had *kelloggi* responded in appreciable numbers. Obviously few *kelloggi* of either sex responded to the mating calls of the few individuals of their species calling at the site. The limited response can be attributed to any of several differences in the stimuli required to initiate spawning in the two species, or to changes in the physical environment possibly disadvantageous to *kelloggi*, but advantageous for an influx of *retiformis* from the adjacent hills, as suggested above.

Despite the occasional concurrence of breeding seasons in the area of sympatry, the ecological requirements of the two species can scarcely be identical. Dr. Frederick A. Shannon has generously supplied information obtained near Hermosillo in 1957 and 1958 that provides suggestive, though inconclusive, evidence of differences. While traveling the road westward toward Puerto Kino early in the evening (*ca.* 8.55 P.M.) on July 24, 1957, Shannon reports that he encountered *Bufo kelloggi*. He obtained three specimens within 8 miles of Hermosillo, but saw no *retiformis*. On August 4 of the following year he collected seven specimens of *retiformis* at distances of from 5.5 to 10.5 miles west of the city, after leaving Hermosillo at 9.15 P.M., when the air temperature of 32.6° C. was recorded. At 10.00 P.M., when Shannon was 26.2 miles west of the city, he encountered heavy rains. At this hour, when air temperatures approximated 30° C., *retiformis* was still abroad at this locality. The storm ceased at 10.45 P.M. but began again around midnight. By then Shannon had turned around and was traveling eastward on the route covered earlier in the evening. On the return trip, however, after the air temperature had descended to 25.8° C., he saw no more *retiformis*, but found *kelloggi* abroad, 16.5 miles west of Hermosillo, where Shannon obtained 11 specimens.

These observations raise questions for which satisfactory answers cannot yet be given. Perhaps *B. kelloggi* differs from *retiformis* in requiring (1) lower temperatures, (2) heavier rains, or (3) the accumulation of larger quantities of water on the surface before breeding occurs. Though relatively few data are available, it is questionable whether differences in the air temperatures account for the later appearance of *kelloggi* on the night when Shannon recorded the information, for *retiformis* is known to call both west and north of Hermosillo at air temperatures of, respec-

tively, 22.5° C. and 24° C. In the same area *kelloggi* was breeding when the air temperature was 22.5° C., and near San Blas, Sinaloa, Zweifel recorded a chorus following a heavy rain at 4.00 P.M., when toads of the species were in shallow water at 25.5° C.

Possibly *B. kelloggi* breeds more often during or immediately following heavy rains, whereas the adaptations of *B. retiformis* dictate a delay in its

TABLE 1

VARIATIONS IN MEASURABLE CHARACTERISTICS OF THE MATING CALLS OF TOADS IN THE *Bufo debilis* GROUP

(An asterisk indicates the calls for which spectrograms are illustrated in fig. 2.)

Species and Locality	Air Temperature (in Degrees Centigrade)	Emphasized Frequency (in Cycles per Second)	Duration, Mean and Extremes (in Seconds)	Pulsations per Second
Bufo debilis insidior				
1 mile NE. of Rodeo, New Mexico, in Arizona	17.0	3500–3800	4.5 (4.0–5.2)	108
8 miles N. of Rodeo, New Mexico	18.5	3600–3900	5.27 (4.9–5.7)	112
*5 miles NE. of Rodeo, New Mexico	20.5	3500–3700	6.1 (5.5–7.4)	124
Near Apache, Arizona	20.3	3500–3700	3.0 (2.0–3.6)	124
Near Apache, Arizona	20.3	3450–3600	4.2 (3.6–4.7)	124
Bufo retiformis				
* 11.5 miles S. of Hermosillo, Sonora	22.5	3400–3700	2.6 (2.0–3.2)	184
11 miles N. of Hermosillo, Sonora	24.5	3500–3800	2.3 (1.9–2.5)	224
11 miles N. of Hermosillo, Sonora	24.5	3400–3700	1.9 (1.1–2.4)	224
Bufo kelloggi				
* 18 miles W. of Hermosillo, Sonora	22.5	3900–4600	2.8 (2.4–3.6)	132
Near San Blas, Sinaloa	25.5	4300–4400	3.0 (2.3–3.8)	132

response that allows sufficient time for pools of greater stability to form. If so, the few *kelloggi* Zweifel observed in the large chorus of *retiformis* on July 30, 1958, represented stragglers from an earlier aggregation of *kelloggi*. Interpretation of the data presently available must remain speculative, however, though Shannon's observations certainly suggest differences in the responses of two species to changes in the physical environment.

Divergence in Mating Calls

Data for mating calls of representative populations of the three species of toads in the *Bufo debilis* group are summarized in table 1. Pulsation rates were ascertained from sound spectrograms made with the Sona-Graph. Calls were timed with a stopwatch while being reproduced from taped recordings, at one-fourth of the normal speed to insure greater accuracy. Additional data and sound spectrograms (fig. 2) derived from recordings of the mating calls reproduced at normal, as well as at one-fourth of the normal, speeds disclose differences not mentioned in a brief discussion of the status and relationships of these toads published earlier (Bogert, 1960).

Stebbins (1951), who obtained data from a population north-northeast of Douglas, Arizona, described the mating call of *Bufo debilis insidior* as a rapid, cricket-like trill sustained at one pitch, and prolonged for periods ranging from three to seven seconds when the substratum temperature was 20.4° C. Blair (1956) described the call of Texan populations (from Valentine, Silver, and Throckmorton, hence including the nominate subspecies as well as *insidior*) as a high-frequency buzz, ranging in duration from two and two-tenths to seven and two-tenths seconds. Emphasized frequencies ranged from 3180 to 3600 cycles per second, at air temperatures between 14° C. and 25° C. The pulsations per second Blair reports for the populations in Texas range from 84 to 128, with both extremes reported for toads in the Throckmorton population at the air temperature of 14° C. At two other localities, where air temperatures were 23.0° C. and 25.0° C., pulsation rates were 120 to 124 per second, respectively.

Savage (1954) described the call of *B. retiformis* as "a rising crescendo of a single drawn-out note, not unlike the buzzer on an electric alarm clock, with a slight trill giving the effect of a vibrating police whistle." He added that the call "lasts about five seconds, dropping off in tone and intensity near the end." Sound spectrograms (fig. 2) of the mating call disclose a sharp rise in frequencies at the very beginning, but toward the end there is no change in either the frequency or the intensity of the call. The maximum duration of any call recorded in the Hermosillo region is three and two-tenths seconds. The mating calls of *B. retiformis* and *B. d. insidior* may be heard on a commercial recording (Bogert, 1958), in which the call of *insidior* is reproduced at three speeds, at the standard record speed of 33 ⅓ revolutions per minute.

As can be seen in table 1, there are variations in the pitch (or emphasized frequencies) and duration of mating calls of each species, with

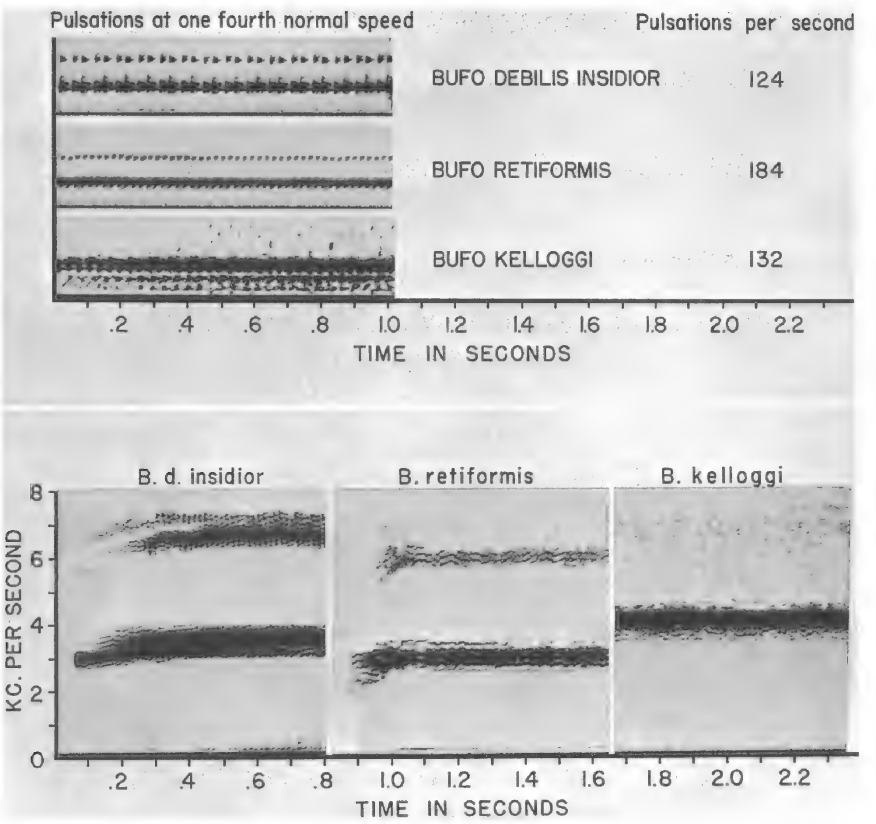

FIG. 2. Sound spectrograms illustrating mating calls of toads in the *Bufo debilis* group, with calls reproduced at subnormal speeds, to show details of pulsations, and at normal speeds, with the pitch indicated in kilocycles per second in scale at left. Documentary notes for calls shown are included in table 1.

differences between means for the durations of calls uttered by individuals participating in the same chorus. Pulsation rates may vary from one population to another, as reported for other species of *Bufo* (Blair, 1956; Bogert, 1960).

Various authors cited by Bogert (1960) have shown that within the same species mating calls vary in frequency, duration, and the pulsation rate, depending in part on the body temperatures and the size of the individuals emitting the sound. Though spectrographic analysis reveals several exceptions, the pitch tends to be higher in smaller species. Infraspecific variations in pitch are sometimes attributable to differences in the size of individual males in the same chorus. Toads of the *debilis* group,

like those of other species that produce prolonged trills, often call at irregular intervals, with extensive variation in the duration of the calls in any sequence. Despite variations in the duration and the pitch, the pulsation rates of calls at any one locality usually tend to be identical, or nearly so when issued by males at similar body temperatures.

Slight differences in the body temperature perhaps account for small deviations observed in pulsation rates of calls recorded under conditions in which nothing better than air temperatures could be obtained to document them. When toads call from pools, their body temperature closely approximates that of the water, but on land the body temperature may differ a degree or so from that of the substratum or the air, depending on the relative humidity. When the atmosphere is nearly saturated shortly after a rain, the temperatures of the air, the substratum, the water in smaller pools, and the toad may be virtually identical. It is preferable, but not always possible, to record the air temperature just above the substratum near the toad issuing the call that is being recorded. Body temperatures, of course, provide more reliable data whenever it is feasible to capture a toad immediately after recording its voice. In the handling of small toads, however, heat from the hands may be transferred to the toads, even when precautions are taken to avoid prolonged contact. Nevertheless, inaccuracies in the recording of temperatures seldom account for wide departures from the mean for any characteristic of calls. Hybrids not readily distinguished as such, or individuals with aberrant voices, account for marked differences in pulsation rates occasionally encountered.

Differences in body temperatures may nevertheless explain the extraordinarily wide range in pulsation rates Blair (*supra cit.*) reported for three calls of *B. debilis* at Throckmorton, Texas, even though all three were recorded at the air temperature of 14° C. Water temperatures at the time were 5° higher, however, and if the toads calling at pulsation rates of 125 and 128 were partly submerged, it is conceivable that the toad issuing the call at the much lower rate of 84 pulsations per second was on land. If the relative humidity was exceptionally low, evaporation from the mucus-covered skin could have caused its body temperature to be appreciably lower than that of the air. Relative humidities are seldom low enough at the substratum level near pools to cause toads to be subjected to excessive evaporation. Hence it is equally probable that the toad with a pulsation rate of 84 was abnormal for the population.

Whatever the explanation for the low pulsation rate may be, when allowance is made for differences in the thermal levels, pulsation rates in the mating calls of *Bufo debilis insidior* recorded in Arizona and New

Mexico approximate those of the majority of the calls Blair reported for Texan populations of *Bufo debilis*. The data for *insidior* in table 1 are derived from recordings made at four localities, within a distance of 20 miles in San Simon Valley of Arizona and New Mexico. The calls were taped at intervals over a five-year period, at air temperatures ranging from 17.0° C. to 20.5° C. Pulsation rates, which vary with the temperature, range from 108 to 124.

Bufo kelloggi was recorded at slightly higher air temperatures, 22.5° C. in Sonora and at 25.5° C. farther south in Sinaloa. The difference in air temperatures at the two localities may or may not accurately reflect differences in body temperatures, however, for a pulsation rate of 132 appears in spectrograms of both calls. This rate is not appreciably higher than that obtained for *B. d. insidior* at air temperatures 2° or 3° lower. It is doubtful, therefore, whether there are significant differences in pulsation rates between the calls of the allopatric species *B. kelloggi* and *B. debilis*.

The situation differs when the calls of species occurring sympatrically are compared. *Bufo retiformis* issues calls with pulsations that vary from 184 to 224 per second at air temperatures of between 22.5° C. and 24.5° C., in contrast to 132 pulsations per second in the calls of *kelloggi* at air temperatures of 22.5° C. and 25.5° C. Slight differences in the detailed structure of the calls of each of the three species are discernible in spectrograms, when the voices are reproduced at one-fourth of the normal speeds. Spectrograms disclose infraspecific variations, however, which suggests that little emphasis should be placed on such details.

Similarly, when the variations are taken into account, little importance should be attached to the relatively slight differences between the means for emphasized frequencies and the durations of the calls of the three species. The differences between pulsation rates in the calls of *kelloggi* and *retiformis*, however, are sufficiently pronounced to warrant assumptions that calls distinctive in this respect may aid in discouraging interspecific matings where the two species occur together. Pulsation rates appear to be of greater significance than other characteristics of mating calls, whether individual females utilize vocalizations in locating receptive males of their own species, or both males and females orient their movements when attracted by choruses, but utilize other means of species discrimination after both sexes reach the spawning site. It has been suggested (Bogert, 1960) that the vocalizations of many, but not all, species of *Bufo* serve primarily to assemble receptive males and females in breeding aggregations, in which mating calls play a subordinate role in species discrimination. If this hypothesis proves to be correct, *retiformis* and *kelloggi* presumably assembled in separate breeding aggrega-

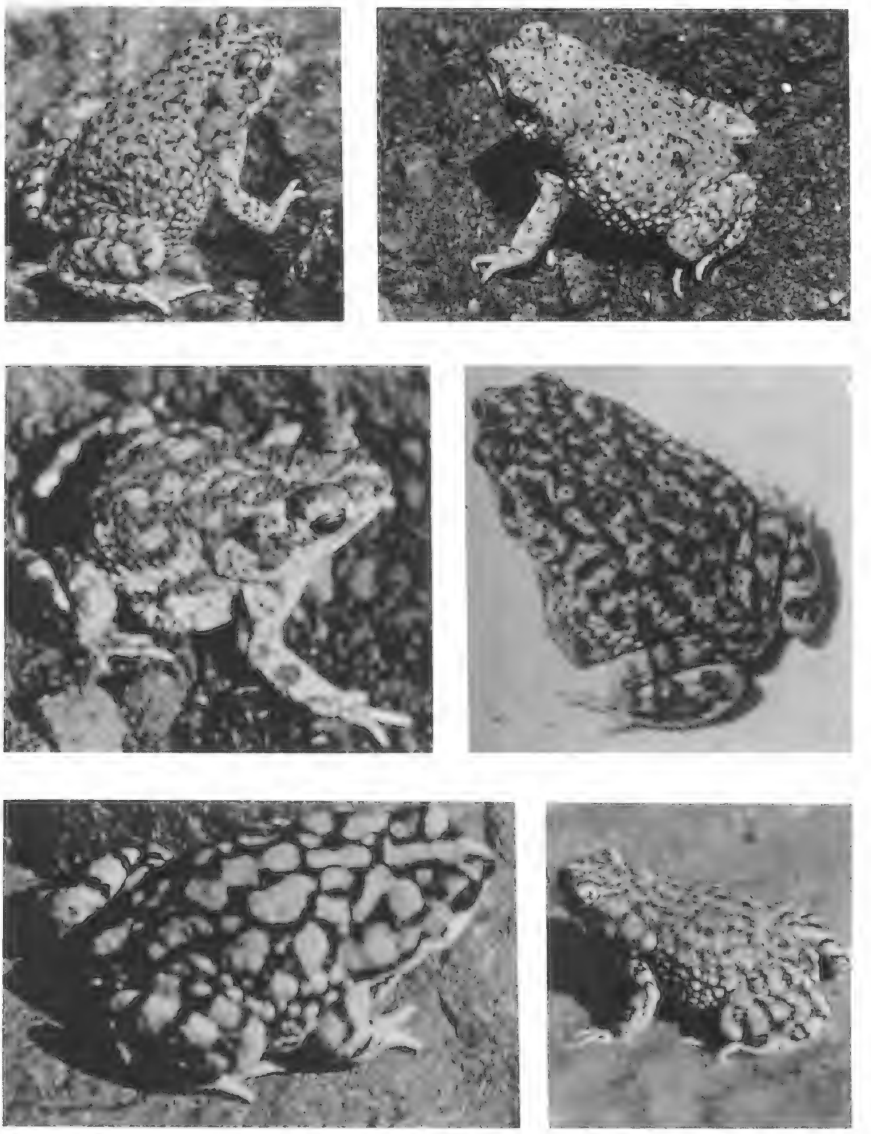

FIG. 3. Living examples of toads of the *Bufo debilis* group. *Top, left: Bufo d. insidior* from near Portal, Arizona. *Top, right: Bufo d. debilis* from Quemado, Texas. *Middle, left: Bufo kelloggi* from 11 miles north of Vicam, Sonora. *Middle, right: Bufo kelloggi* from 17 miles west of Hermosillo, Sonora. *Bottom, left: Bufo retiformis* from 5 miles south of Hermosillo, Sonora. *Bottom, right: Bufo d. insidior* from Jornada State Game Refuge, New Mexico.

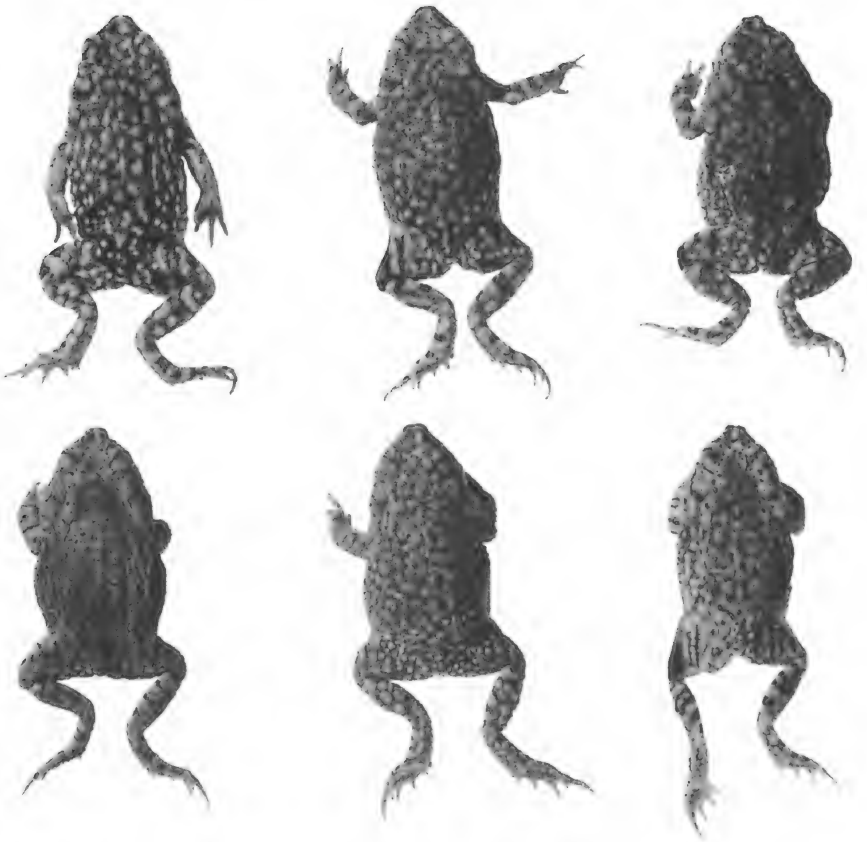

FIG. 4. *Bufo debilis insidior*. Specimen in middle of upper row from Elfrida, Sulphur Springs Valley, Arizona; others from San Simon Valley near Rodeo, New Mexico.

tions prior to modifications in the habitat resulting from man's agricultural activities in the terrain west of Hermosillo. In other words, ecological barriers that once curtailed interbreeding between the species may be in a state of flux because of the changing environment. In the absence of such barriers, ethological divergence may effectively inhibit gene exchange, or limit it to fortuitous mismatings.

MORPHOLOGICAL DIVERGENCE

Despite evidence that toads of the three species do not differ appreciably in body proportions (Savage, 1954), measurements of snout to vent

lengths reveal differences between the means for the species, if males and females are treated separately when samples are compared. The extent of the difference, however, depends on the sources of the toads that comprise the samples. Sanders and Smith (1951) did not compare means, although they called attention to the larger toads encountered in both subspecies of *debilis* in the populations near the southern extremities of their respective ranges in Mexico. They reported that males and females of *B. d. debilis* attained maximum sizes of 39 and 50 mm., respectively, whereas Savage (1954) reported maximums of 42 mm. for males and 48 mm. for females in a sample restricted to 48 specimens from Oklahoma and Texas. For *B. d. insidior* Sanders and Smith indicated maximums of 45 and 54 mm. for males and females, respectively, which agree fairly well with the figures (42.0 and 51.5 mm.) Savage provided for material examined, which included individuals taken as far south as Durango in Mexico.

If the series of *B. d. debilis* from Texas and Oklahoma contains toads as large as those Sanders and Smith reported for Mexico, it is evident that northern populations of the nominate subspecies contain individuals nearly as large as those encountered to the south. The average size for adults in individual populations of all three species probably reflects adaptive responses to localized environments. Where clines in this character exist, it is doubtful whether they are simple directional trends from south to north. Relatively small samples from a few localities suggest a mosaic distribution in the average adult size of *kelloggi*, which may not be borne out with larger series. Savage provided means and extremes for the snout to vent length of the species and subspecies of the *debilis* group. His study was hampered, however, by the small samples of *kelloggi* and *retiformis* available at the time.

A total of 42 specimens of *retiformis* more recently obtained in Sonora includes only 15 females, but the snout to vent length of some of these is at least 10 mm. greater than Savage could report, with only three females in his sample. Males from the vicinity of Hermosillo, however, are approximately the size of specimens Savage reported for populations farther north. Larger samples of *retiformis* are likely to require revisions in the mean and extremes for body dimensions of both sexes. Inexplicably, however, Savage reported means as well as maximums for four males and nine females of *kelloggi* that exceed those obtained for snout to vent measurements of 26 males and 16 females from Sonora, Sinaloa, and Nayarit. Specimens of *insidior* obtained mainly in San Simon Valley in New Mexico and Arizona disclose greater differences between the sexes and a higher mean for the snout to vent length than Savage reported for specimens

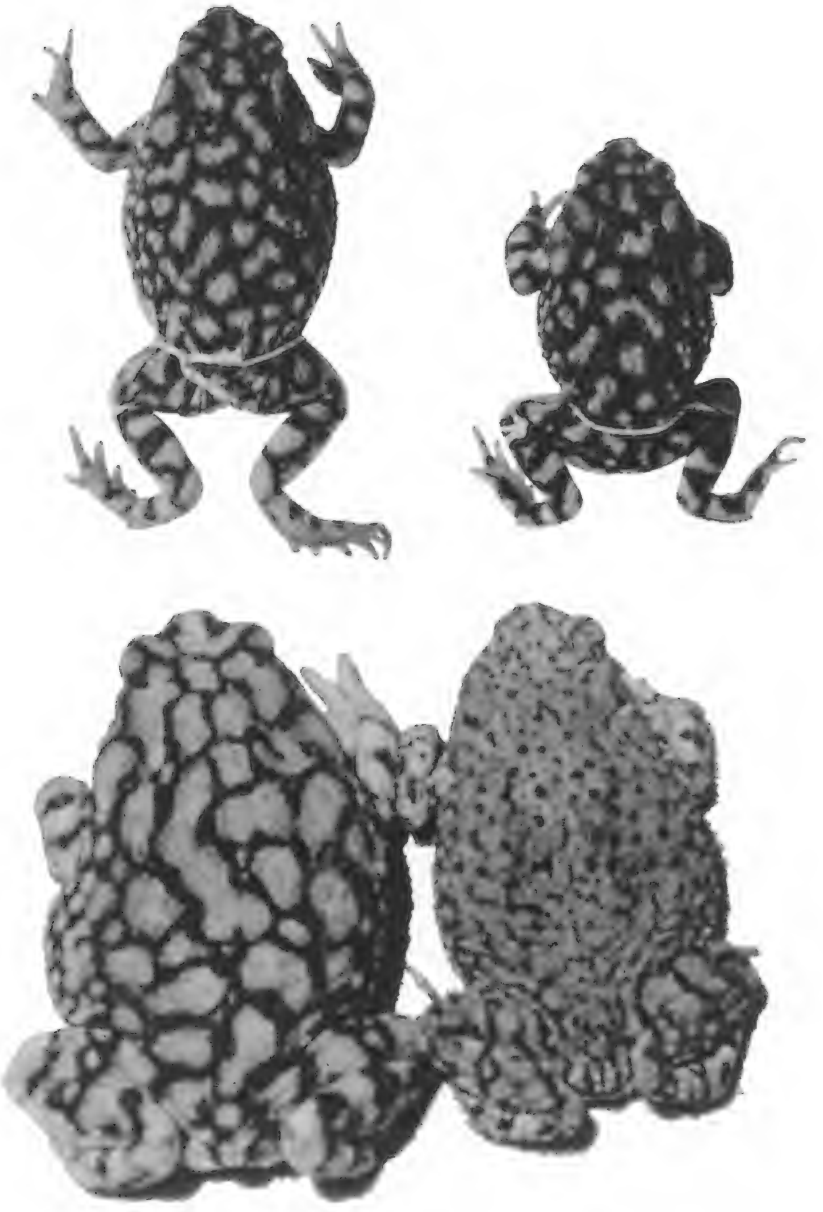

FIG. 5. *Upper, left: Bufo retiformis* female. *Upper, right: Bufo retiformis* male. Both from La Playa, Sonora. *Lower:* Living females of near maximum size: (*left*), *B. retiformis* from 5 miles south of Hermosillo, Sonora; (*right*), *B. d. insidior* from near Rodeo, New Mexico.

drawn from a number of localities within the range. His figures, derived from samples perhaps more nearly representative of the subspecies as a whole, are employed for *insidior* in the following tabulation.

The means of the measurements (in mm.) from snout to vent, with extremes in parentheses, are:

Bufo d. insidior
Males 35.1 (32–42)
Females 36.5 (28–52)
Bufo retiformis
Males 44.4 (39–47)
Females 52.5 (46–57)
Bufo kelloggi
Males 32.7 (29–36)
Females 37.4 (29–44)

Though relatively useless taxonomically, body size often appears to be subject to natural selection and hence is dependent on the effects of local environments of isolated or semi-isolated populations within the range of the species. Differences in the size of sympatric congeners often make it difficult or virtually impossible for the males of one species to clasp females of the other. It is noteworthy, therefore, that means for snout to vent measurements reveal *retiformis* to be a larger toad, with a mean length appreciably exceeding that of *kelloggi*, by 11.7 mm. in males, and by 15.1 mm. in females. It is questionable whether males of *retiformis*, which normally clasp females with a bulk greater than their own, would readily seize any but the larger females of *kelloggi*. The females of *retiformis*, with an average body length nearly one and a half times that of *kelloggi* males, greatly exceed them in body mass, particularly at spawning sites where receptive females are distended with eggs following ovulation.

Such discrepancies in size may discourage mismatings, but in this instance, it is questionable whether the size differential alone would effectively block gene flow in the absence of other isolation mechanisms. Differences in the average adult size of the two species may be reënforced through selection in sympatric populations following prolonged contact of the two species. Samples of *kelloggi* from the area of overlapping ranges are comprised largely of males, of which the mean snout to vent length is but 0.7 mm. below that for males from all portions of the range. For males of *retiformis* the mean for snout to vent length in populations near Hermosillo is but 0.6 mm. above that Savage (1954) reported for populations in Sonora well to the north of the zone of sympatry.

Without experimental evidence, it is conjectural whether species discrimination depends to any significant extent upon differences in pattern,

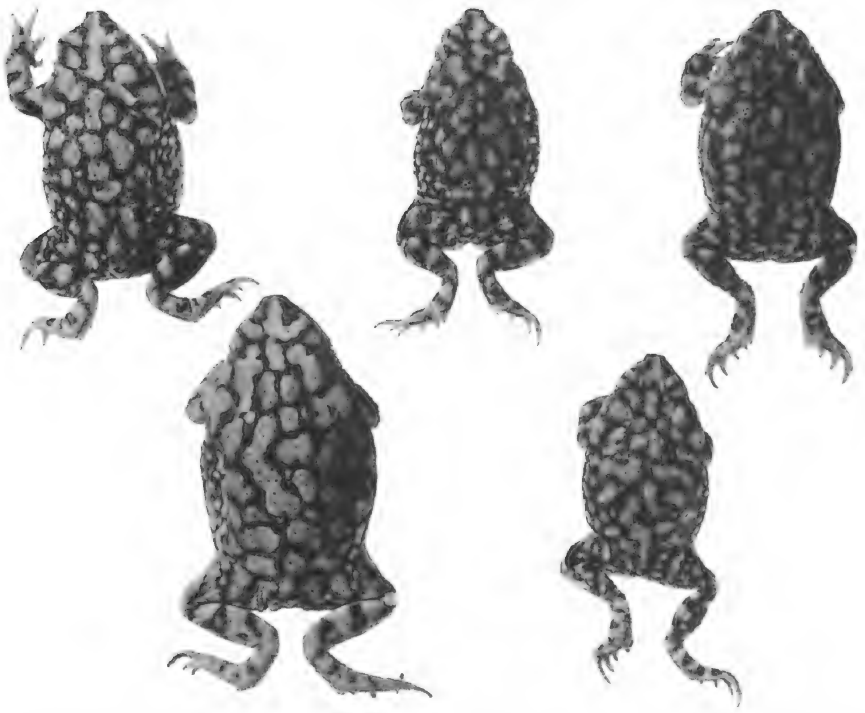

FIG. 6. *Bufo retiformis* from localities 5, 7, and 11.5 miles south of Hermosillo, Sonora. Larger specimen at lower left female; others, males.

coloration, or pustulation when two species occur in mixed breed aggregations. Numerous reports indicate that, when sexually aroused, male toads often clasp other amphibians, including larval salamanders (Bogert, 1958) or even inanimate objects. It may seem improbable, therefore, that male toads at spawning sites employ tactile cues to discriminate between species when clasping females.

Such an assumption may be unwarranted if the male responds to tactile stimuli that depend for their effectiveness on the movements of the female following amplexus. When sexually aroused in a breeding aggregation, male toads indiscriminately clasp other individuals of either sex. When another male is seized, it responds by producing release vibrations and struggles to obtain its release, normally with success. In contrast the receptive female is relatively passive, though she commonly moves to reach the site where her eggs will be deposited. While the male is in amplexus, with much of its ventral surface pressed against the back of the female, the nature of the tactile stimuli resulting from her movements

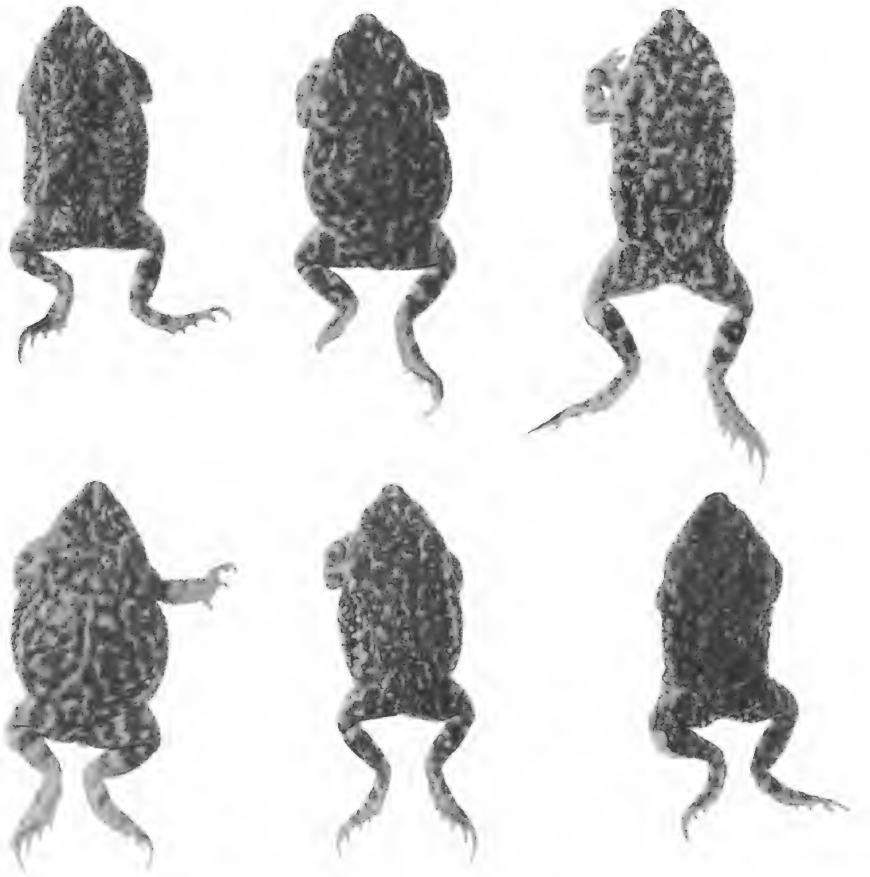

FIG. 7. *Bufo kelloggi* from 17 miles west of Hermosillo, Sonora.

may depend on the texture of the female's skin. If so, it is conceivable that suitable stimuli induce the male to retain his grip or, when such stimuli are absent, to release the female prior to oviposition.

There is virtually no evidence that visual or olfactory cues play any significant role in species discrimination, though few investigators devise experiments that satisfactorily reveal which sensory mechanisms are involved. Vision, though perhaps subordinate to other senses, plays some part in mating activities (Bogert, 1960). Species of *Bufo* with sympatric distributions commonly differ conspicuously in their pigmentations and patterns, as well as in pustulation, even when there are no marked differences in size or proportions. Many differences between species, of course, are attributable to the combined effects of selection and genetic drift

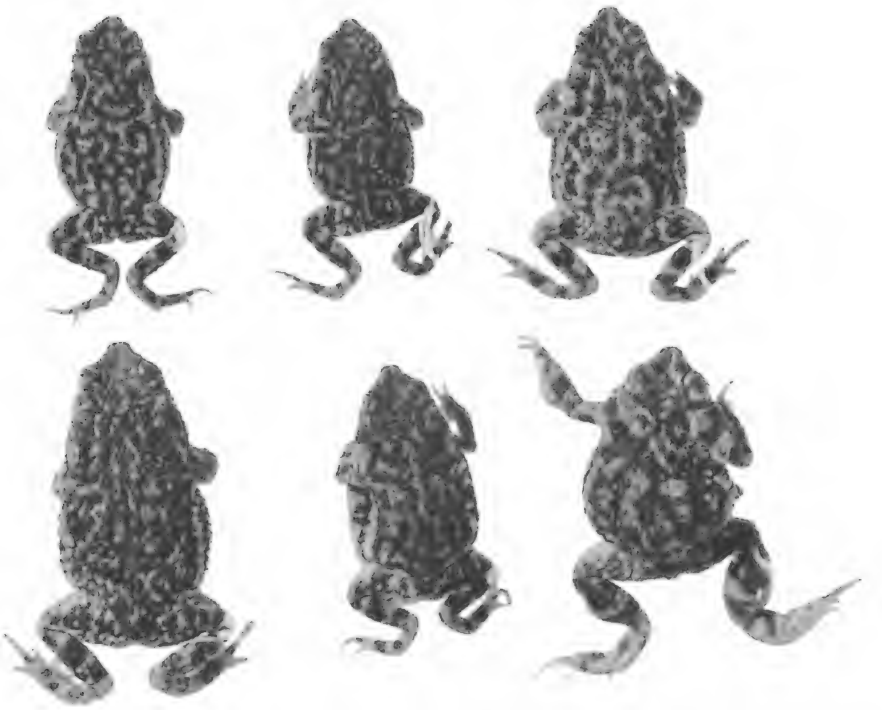

FIG. 8. *Bufo kelloggi* from 11 miles northwest of Vicam, Sonora, examples mistakenly assumed to be intergrades with *Bufo retiformis*.

during antecedent periods of isolation. Hence relatively few morphological characteristics are likely to be directly associated with patterns of behavior that allow species to maintain their integrity.

As indicated or implied in earlier discussions, mean differences between populations within the species presumably stem from adaptations that provide for optimal fitness to local environments. A rough index to the genetic diversity of individuals that comprise such populations is readily obtained by a study of external structures, a procedure taxonomists employed even before they were fully cognizant of the evolutionary significance of intraspecific variations. Savage (1954) attempted to summarize the variations in toads of the *debilis* group, and he showed mean differences in the size of adults of the three species, even though they have virtually the same proportions. Consequently he relied heavily on qualitative differences, though he was forced to describe the variations in his efforts to diagnose the forms he recognized. He supplemented his discussion with diagrammatic illustrations of representative patterns, but

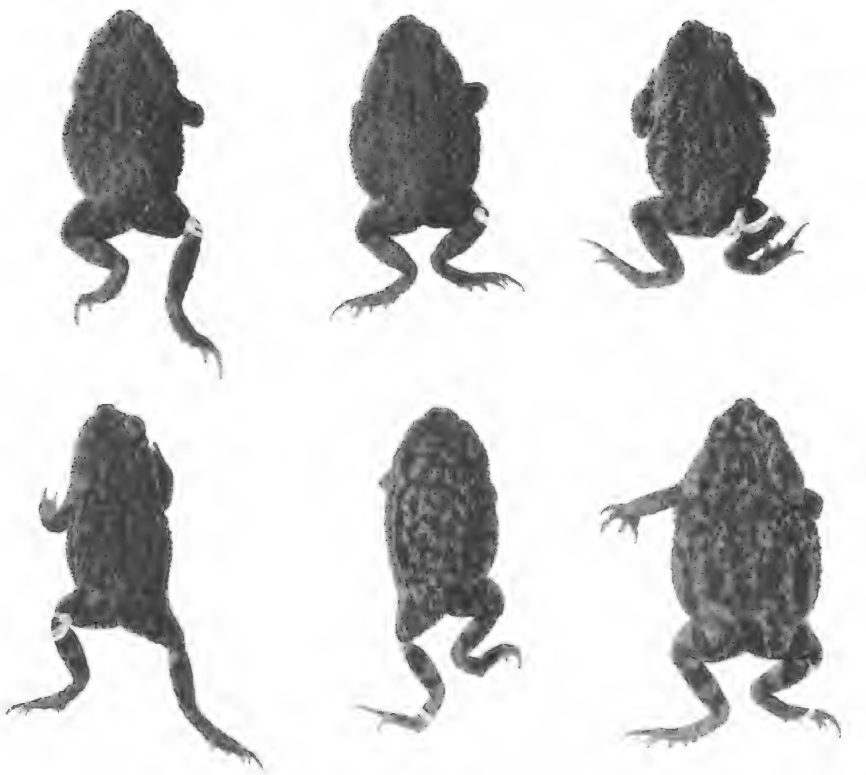

FIG. 9. *Bufo kelloggi* from 1.8 miles southeast of Vicam, Sonora.

these oversimplify the extent of the variation. Riemer's (1955) conclusion that toads in the population of *kelloggi* near Vicam, Sonora, were intergrading with *retiformis*, though based in part on erroneous concepts of the distributions, revealed the shortcomings of the diagnoses, keys, and descriptions Savage was able to offer.

Inadequacies were inevitable with the limited material available in 1954. Populations perhaps remain to be discovered that will not conform to any with the range of variation noted here. Nonetheless, the three species of toads are readily separable on the basis of pattern and coloration, if due allowance is made for intraspecific variations and superficial similarities. The pattern of *B. d. insidior* consists of dots and bars that may or may not coalesce in varying degrees, in some individuals to form a reticulum, as Savage indicates. Contrary to impressions derived from his diagrams, however, the lighter areas enclosed in the coarser dark reticulum of *retiformis* are roughly double the area of those in *insidior*, in pro-

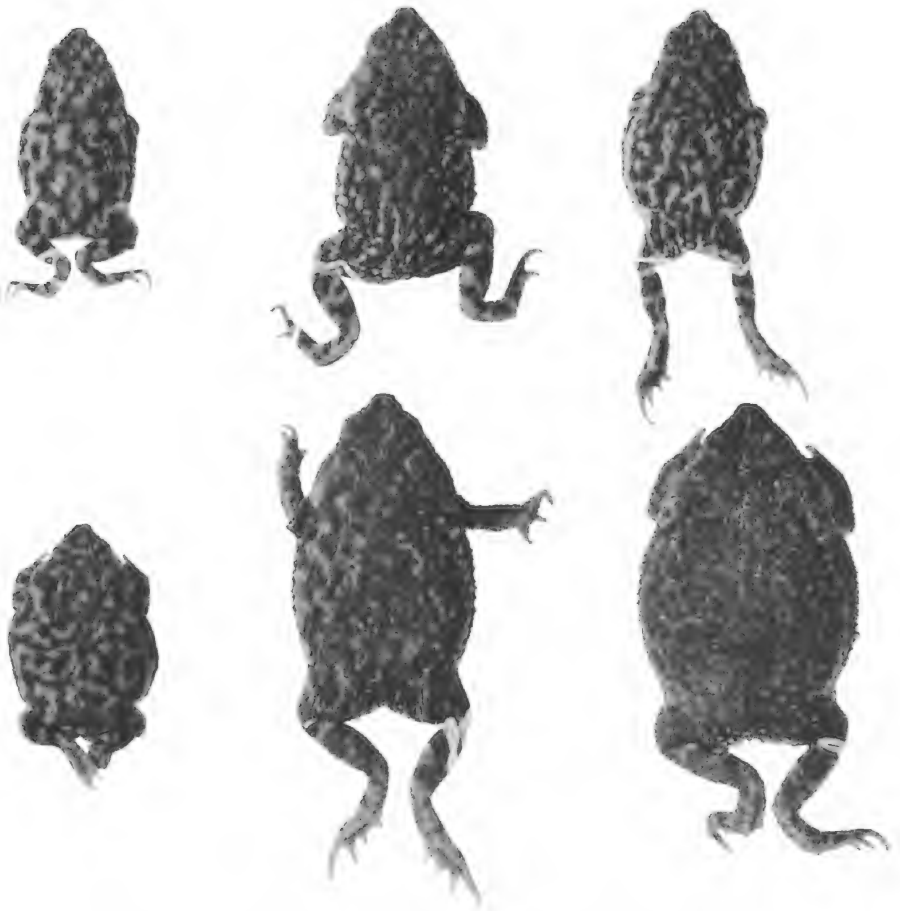

FIG. 10. *Bufo kelloggi* from 3.8 miles south of Vicam, Sonora.

portion to the size of the toad. In contrast, *kelloggi* is more aptly described as being mottled rather than reticulated, though the lighter markings may either be well defined or obsolescent. Photographs of individuals from representative populations of the three species (figs. 3 to 11) convey a fair notion of their patterns and their variability. These are perhaps more useful as a means of identifying specimens than keys requiring lengthy descriptions.

LEVELS OF DIFFERENTIATION

This study is concerned primarily with the extent of the differentiation, and hence also with the taxonomic status, of toads of the *Bufo debilis* group

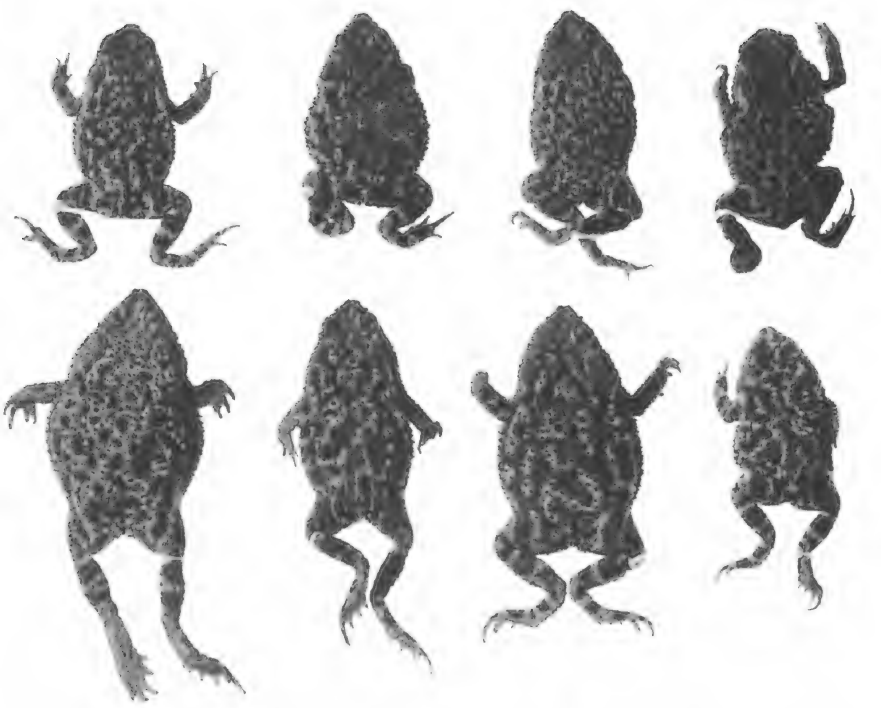

FIG. 11. *Bufo kelloggi*, individuals at the extreme right of each row from Acaponeta, Nayarit; others from 2 miles north of Mazatlán, Sinaloa.

on the Pacific drainage. The conclusions reached are based on evidence herewith summarized. It may be noted, however, that the distribution of *Bufo debilis* on the Atlantic drainage is essentially or potentially continuous, with the nominate subspecies restricted to regions more humid than those occupied by *B. debilis insidior*. The transition from *debilis* to *insidior* (see representatives depicted in fig. 3) can scarcely be so abrupt as Savage (1954) indicated, but differentiation in external morphology has perhaps reached a level that warrants recognition of two subspecies, as earlier authors advocated.

It is highly improbable that the distributions of *Bufo d. insidior* and *Bufo retiformis* are (or will prove to be) contiguous in Arizona and Sonora, as mapped by Sanders and Smith (1951) and by Savage (1954). The disjunct distributions of *retiformis* and *insidior*, the ranges of which are separated by a distance of approximately 100 miles, preclude any great likelihood of their intergradation. Contrary to the speculation of Sanders and Smith, however, the distributions of *retiformis* and *kelloggi* overlap

along the periphery of the coastal plain in central Sonora. Though only one specimen of *retiformis* has been taken near the coast north of Guaymas, presumably close to the southern extremity of its range, the species appears to occupy an elevated area between disjunct populations of *kelloggi*.

Despite sporadic occurrences of members of both species at the same spawning sites, and no indication of differences in breeding seasons, gene exchange between *kelloggi* and *retiformis* appears to be inhibited if not effectively blocked by an array of isolation mechanisms. These include dichotomous differences in their calling habits, the pulsation rates of their respective mating calls, and discrepancies in their size and external morphology. Limited evidence points to differences between the responses of toads in sympatric populations to changes in the physical environment; *kelloggi* breeds during or immediately following rains, whereas the mating activities of *retiformis* commonly await the formation of larger pools. The two species occupy separate habitats elsewhere, but changes wrought by man in the coastal plain where *retiformis* and *kelloggi* occur together west of Hermosillo, Sonora, may account for the larger toad's recent invasion of habitats previously occupied by *kelloggi*. Whether the two species are genetically incompatible remains to be established.

The existence of several premating isolation mechanisms does not preclude hybridization on rare occasions. In fact, Frederick Shannon (*in litt.*) mentions specimens taken west of Hermosillo that he regards as hybrids. He may well be correct, though no specimens that I have examined possess characters in combinations that suggest a hybrid origin. Not all hybrids are readily detected by their external appearance, however, for individual male toads closely resembling *Bufo woodhousei fowleri* produced mating calls that to human ears bore greater resemblance to the calls of *Bufo americanus*. The duration of the calls and data obtained from spectrographic analysis showed clearly that the toads were hybrids of the two species (Bogert, 1960). In some instances hybrids are readily recognized, for example, those between *Bufo cognatus* and *Bufo mazatlanensis*, reported from Sonora (Bogert, 1960). In any event, the sporadic occurrence of hybrids between sympatric species does not imply that gene flow has been reëstablished between related species derived from a common ancestor. Whatever its shortcomings, all available evidence supports the belief that *retiformis* and *kelloggi* have reached the level of species in the extent of their differentiation in morphology and behavior.

Similarly, there are adequate reasons for considering *retiformis* specifically distinct from *Bufo debilis*. Geographic isolation alone would not serve as a reliable criterion for considering them distinct, for disjunctions occur in the distributions of many amphibians. In this instance there is

ample evidence of differentiation in mean adult size, external morphology, and the pulsation rates of their mating calls. When these differences are taken into consideration, along with the differences observed in their calling behavior, it is doubtful that *retiformis* would interbreed freely with *B. d. insidior*, even if they inhabited the same area and their breeding seasons were identical.

The remote possibility exists that collecting in east-central Sonora will disclose annectant populations intermediate between *kelloggi* and *insidior*. Relatively little divergence in their mating calls, habits, and behavior leaves doubts concerning their effectiveness in discouraging interbreeding between the two. Despite extensive variations in both species, they are nevertheless morphologically distinct, and, moreover, adapted to distinctive habitats. Until those portions of Sonora where no toads of the *debilis* group have been taken are visited by herpetological collectors, it is eminently preferable to assume that *kelloggi* and *insidior* are specifically distinct.

To summarize the taxonomic implications of this review, the following names should be employed for toads of the *Bufo debilis* group:

Bufo debilis debilis Girard, 1854
Bufo debilis insidior Girard, 1854
Bufo kelloggi Taylor, 1938
Bufo retiformis (new combination), Sanders and Smith, 1951

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It is a pleasure to thank Sr. Ing. Luis Macias Arellano, Director General in charge of the Dirección General de Caza, Departamento de Conservación de la Fauna Silvestre, Secretaría de Agricultura y Ganadería, whose courteous cooperation in issuing permits to collect in Mexico enabled us

to obtain the specimens and data requisite for the solution to many problems. The work in Sonora was undertaken while other studies were being pursued with the partial support provided by a fellowship from the John Simon Guggenheim Memorial Foundation.

Finally I am grateful to Mrs. Margaret Shaw, whose efficiency, patience, and attention to detail contributed so much to the preparation of the manuscript.

LOCALITY RECORDS

The list that follows represents records known for the three species within the area covered. It includes (1) specimens recorded in the literature, with the source indicated, as well as (2) those in the collection of Frederick Shannon of Wickenburg, Arizona (F.A.S.), and those in the collection of the American Museum of Natural History (A.M.N.H.). With few exceptions, I have examined those listed by number, in addition to others in the Museum of Vertebrate Zoology, at the University of California (M.V.Z.). A few specimens Shannon obtained in 1959 were not examined, though he supplied identifications and the locality data for those included in the list. A single specimen of *Bufo retiformis* in the collection of the Museum of Zoology, University of Michigan (U.M.M.Z.), was examined.

In those instances in which collectors use place names several miles distant from sites of collection, the data have been revised to indicate distances from towns closer to the site where specimens were taken. Thus a record for *Bufo debilis insidior* previously listed as "30 miles south of Cochise," when it is known that the distance represents the mileage on the highway, is now listed as "5 miles east of Pearce." A record for *Bufo kelloggi* published as being "30 miles SSW of Navajoa [*sic*]" would be plotted in the Pacific Ocean if taken literally. Hence it is assumed that the toad came from an area along the highway southeast of Navojoa, and listed as taken "4 miles southeast of Masiaca."

It will be noted that in a few instances localities are so close that one symbol on the map (fig. 1) is sufficient to cover all those within a limited area. Thus there are fewer localities indicated on the map than I have listed below.

BUFO RETIFORMIS

United States

Arizona

Pima County

11 miles south of Ajo; Williams and Chrapliwy, 1958

12.5 miles south of Ajo; Williams and Chrapliwy, 1958
14.4 miles south of Ajo (type locality); Sanders and Smith, 1951
17.5 miles south of Ajo; Williams and Chrapliwy, 1958
Gunsight Hills, A.M.N.H. Nos. 60671, 59189, plus three untagged
3 miles southwest of Hickiwan; Williams and Chrapliwy, 1958

MEXICO

Sonora
1.5 miles west of Altar; Savage, 1954
16 miles northwest of La Playa, A.M.N.H. Nos. 55351, 55352
26.7 to 21.7 miles west of Hermosillo, F.A.S. Nos. 12573, 12574
22.5 miles west of Hermosillo, F.A.S. Nos. 12551–12556, A.M.N.H. Nos. 62688–62697
16 miles north of Hermosillo, A.M.N.H. Nos. 65777, 65778
11 miles north of Hermosillo, A.M.N.H. Nos. 65774–65776
5 miles south of Hermosillo, A.M.N.H. Nos. 58342, 58343, 58346, 58347 (skeleton)
7 miles south of Hermosillo, A.M.N.H. Nos. 58344, 58345
11.5 miles south of Hermosillo, A.M.N.H. Nos. 58340, 58341
2.5 miles north of Rancho Noche Buena, U.M.M.Z. No. 117057

BUFO KELLOGGI

MEXICO

Sonora
1 mile to 4 miles north of Hermosillo, F.A.S. No. 12215
22.5 miles west of Hermosillo, A.M.N.H. Nos. 62707–62709
20.5 miles west of Hermosillo, A.M.N.H. No. 62710
20.3 miles west of Hermosillo, A.M.N.H. No. 62711
17.0 miles west of Hermosillo, A.M.N.H. Nos. 58348–58358
15.5 to 10.5 miles west of Hermosillo, F.A.S. Nos. 12565–12570
10.5 to 5.5 miles west of Hermosillo, F.A.S. Nos. 12557–12561
8 to 4 miles west of Hermosillo, F.A.S. No. 12213
Hermosillo, F.A.S. No. 12673
11 miles northwest of Vicam; Riemer, 1955
1.1 miles northwest of Vicam, F.A.S. No. 8101
1.8 miles southeast of Vicam, F.A.S. Nos. 8161–8177
5.8 miles south of Vicam, F.A.S. Nos. 7877–7899
Navojoa, F.A.S. No. 11336
South edge of Navojoa, F.A.S. Nos. 11713, 11714
1.5 miles south of Navojoa, F.A.S. Nos. 13485–13488
3 miles south of Navojoa, F.A.S. Nos. 11698–11709, 11737
3.0 to 5.6 miles south of Navojoa, F.A.S. Nos. 11716, 11717
7.2 miles south of Navojoa, F.A.S. Nos. 11700–11712
8 miles south[east] of Navojoa; Davis and Dixon, 1957
4 miles southeast of Masiaca ("30 miles SSW [?] of Navajoa"); Smith and Chrapliwy, 1958
5 miles southeast of Masiaca, F.A.S. No. 7866
13 miles south of Masiaca; Davis and Dixon, 1957
Ca. 20 miles north of Agiabampo, F.A.S. No. 7866

Sinaloa
24 miles north of Los Mochis; Davis and Dixon, 1957
13 miles north of Los Mochis; Smith and Chrapliwy, 1958
6 miles southwest of San Blas, A.M.N.H. Nos. 59249–59253
"13 to 35 miles north of Culiacán," F.A.S. Nos. 11125–11128
2 miles north of Mazatlán, F.A.S. Nos. 7812–7821, 8945–8948, 8580, 8985–8994, 9051
Mazatlán; Cope, 1889
2 miles east of Mazatlán (type locality); Taylor, "1936" [1938]
6 miles south of Mazatlán, F.A.S. Nos. 11129–11136, 11154
33 miles southeast of Escuinapa; Davis and Dixon, 1957
Nayarit
Acaponeta, A.M.N.H. Nos. 43877, 43878
2 miles southwest of Rosamorada; Chrapliwy, 1956

BUFO DEBILIS INSIDIOR

United States

Arizona
Graham County
16 miles northwest of Pima; Stebbins, 1951
Cochise County
? 15 miles south of Fort Huachuca; Sanders and Smith, 1951
Near Pearce; Savage, 1954
5 miles east of Pearce ("30 miles [via road] south of Cochise"), A.M.N.H. No. 50914
2 miles north of Elfrida, A.M.N.H. No. 58339
10.5 miles north-northeast of Douglas, M.V.Z. No. 49242
4 miles north of Douglas, A.M.N.H. Nos. 65744–65748
2 miles north-northeast of Douglas, M.V.Z. Nos. 49240, 49241
0.4 mile north of Portal, A.M.N.H. Nos. 65751–65754
AVA Ranch, Portal, A.M.N.H. No. 58324
2 to 2.5 miles northwest of Rodeo, New Mexico, A.M.N.H. Nos. 58325–58329, 62722, 62723
Near Chiricahua, A.M.N.H. No. 62724
New Mexico
Hidalgo County
8 miles north of Rodeo, A.M.N.H. Nos. 58331–58338
6 miles north of Rodeo, A.M.N.H. No. 58301
Hatchet Ranch; Sanders and Smith, 1951
Luna County
10 miles north of Florida; Sanders and Smith, 1951
Dona Ana County
23 miles north of Las Cruces; Sanders and Smith, 1951
1 mile north of Jornada Experiment Station; Savage, 1951
Jornada Experiment Station; Savage, 1954
Texas
Brewster County
Alpine; Brown, 1950
14 miles north of Terlingua; Brown, 1950

Culberson County
Van Horn; Savage, 1954
Reeves County
2 miles southwest of Pecos [not in Pecos County, as listed by Brown, 1950]
2 miles southeast of Pecos; Brown, 1950
Toyahvale; Brown, 1950
Weihnacht's Draw; Brown, 1950
Presidio County
11 miles west-southwest of Valentine; Savage, 1954

MEXICO

Sonora
Between Agua Prieta and Fronteras; Savage, 1954
Chihuahua
Río Santa María near Progreso; Sanders and Smith, 1951
1 mile south of Villa Ahumada; Sanders and Smith, 1951
3 miles north of Chihuahua, A.M.N.H. No. 55274
Coahuila
20 miles east of Torreón; Sanders and Smith, 1951
Parras; Fugler and Webb, 1956
Durango
5 miles north of Conejos; Sanders and Smith, 1951
5 miles north of Ceballos, A.M.N.H. No. 64212
Durango; Savage, 1954
Zacatecas
La Colorada; Sanders and Smith, 1951
2 miles south of Majoma; Taylor, "1936" [1938]
10 miles north of Villa de Cos; Sanders and Smith, 1951
15 miles south of Zacatecas; Taylor, "1936" [1938]

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